Social signal learning of the waggle dance in honey bees

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Honey bees use a complex form of spatial referential communication. Their "waggle dance" communicates the direction, distance, and quality of a resource to nestmates by encoding celestial cues, retinal optic flow, and relative food value into motion and sound within the nest. We show that correct waggle dancing requires social learning. Bees without the opportunity to follow any dances before they first danced produced significantly more disordered dances with larger waggle angle divergence errors and encoded distance incorrectly. The former deficit improved with experience, but distance encoding was set for life. The first dances of bees that could follow other dancers showed neither impairment. Social learning, therefore, shapes honey bee signaling, as it does communication in human infants, birds, and multiple other vertebrate species.

ocial learning occurs when one individual learns by observing or interacting with another (*1*) and is particularly useful when complex behaviors must be tuned to specific environmental circumstances or honed by practice or social shaping. For example, human infant babbling and young songbird subsongs are shaped by social feedback into more mature vocal behavior (*2*), and young naked mole rats learn distinctive colony dialects from older rats (*3*). Longer periods of interaction, such as those occurring between parents and offspring, can favor the evolution of such open programs (*4*), which allow novices to acquire skills more rapidly from experienced individuals than they could on their own (*5*). Proficient individuals have had more opportunities to fine-tune their brains and motor outputs to environmental circumstances (*5*); thus, learning from them can be beneficial.

Eusocial insects use social learning, but it is unclear whether this learning shapes their communication, which can be remarkably sophisticated and cognitively complex. *Polistes fuscatus* wasps use social eavesdropping, a form of social learning, to observe conflicts and to assess and remember rivals through facial recognition (*6*). Bumble bees can learn by observation to copy or avoid the foraging choices of other bumble bees through their previous experiences of reward or punishment (*7*). These bees can also learn to obtain a nectar reward by watching their nestmates perform a new behavior and can then innovate and solve the problem more efficiently (*8*). Honey bee workers use social learning when following the waggle dance to learn resource location and quality. However, it has not been previously determined whether dance following can improve the dance performances of young waggle dancers or whether the dance is completely genetically preprogrammed (innate).

The waggle dance is a sophisticated form of spatial referential communication (*9*). The dancer repeatedly circles in a figure-eight pattern centered around a waggle run in which the bee waggles its abdomen as it moves forward (Fig. 1). Referential communication codes information, and the dancer encodes the polar coordinates of a resource relative to the nest. Longer waggle runs communicate greater distances (more retinal optical flow), and the waggle direction angle communicates resource direction. When a bee dances on a vertical comb in the dark, the bee points in the direction of the resource relative to the sun, as transposed to the vertical in relation to gravity. The quality of the food relative to colony need and the dancer's prior experiences (*10*) are encoded in the number of waggle run repetitions and the speed with which the dancer returns to repeat each successive waggle run (*11*).

There is a strong genetic component to the dance: Different honey bee species have distinctive distance encodings (calibrations) that persist even when they are cross-fostered (*12, 13*). An encoding is a curve that describes the relationship between physical distance and the duration of waggle runs for resources at those distances (*14*). Theoretically, novice dancers could benefit by learning from experienced dancers because waggle dancing requires retrieving navigational memory and using detailed motor programs and real-time feedback to translate resource location (*15*). Dances occur on the dance floor, which often consists of colony-specific, uneven, and convoluted comb surfaces (Fig. 1 and fig. S1) (*16*) that dancers must negotiate at relatively high velocities. On average, they cover more than their body length in 1 s (waggle running at
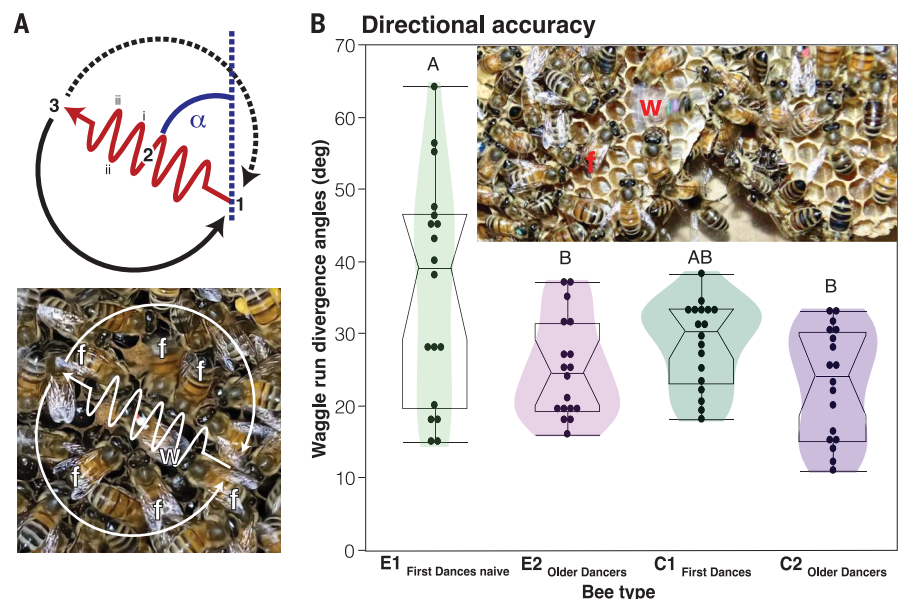
Fig. 1. Waggle dance directional error was highest in the first dances of naive bees that could not follow waggle dances. (**A**) The dancer (w) shakes its abdomen (i-ii-iii, creating one cycle) during the waggle run (1-2-3), whose angle (α) communicates direction, and then makes a semicircular return while being tracked by dance followers (f). (**B**) Divergence error angles decreased with experience in experimental colonies but not in control colonies, in which errors were consistently low (different letters indicate significant differences, Tukey HSD test, *P* < 0.05). (Inset) Dancers typically perform on irregular surfaces that vary between colonies. Data (black circles), notched box plots, and violin plots are shown in all figures.

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15 mm/s and returning back at 20 mm/s) while sensing the positions of their bodies relative to gravity and producing the correct waggle frequency and angle (17). Thus, errors occur. A dancer's successive waggle runs can point to different angles, resulting in directional errors (18). Similarly, waggle runs within the same dance can vary in duration, conveying distance errors (19).

Foragers have the opportunity to learn from more experienced dancers. Workers become foragers as they age: They begin following waggle dancers when they are 8 days old and subsequently perform their first waggle dances when they are 12 days old (20). All workers follow waggle dances before they waggle dance (20), and most follow dances performed by older bees that have previously danced (11). We therefore predicted that the first waggle dances of foragers will exhibit more errors if they are reared in an environment in which they cannot follow other waggle dancers before they begin to dance.

We therefore created colonies in which we observed the first waggle dances produced by foragers (all individually marked and trained to 55% w/v sucrose feeders located 150 m from their colonies) that either could or could not follow other waggle dancers (table S1). Each of our five experimental colonies was established with a single cohort of 1-day-old bees. As these bees aged, we monitored the colonies until we observed the first waggle dances and then observed the same dancers 20 days later when they had more foraging and dancing experience. Naive dancers could not follow any other dancers before their first dances because all bees in the colony were the same age, but as these dancers grew older, they followed other waggle dancers and had more experience dancing. In five control colonies that we established at the same time with adult bees of all ages and in which we observed waggle dancing within 1 to 2 days of colony creation, we measured the waggle dances of control bees at two comparable stages: the first waggle dances in the control colonies ($C1_{First\ Dances}$) and the waggle dances of the same dancers 20 days later when they had more foraging and dancing experience ($C2_{Older\ Dancers}$).

We observed no waggle dancing in all experimental colonies before the first group of bees aged into foraging and dancing ($E1_{First\ Dances\ naive}$; 9.0 ± 2.0 days old). Although we did not track all behaviors of these same bees until 20 days later, when they were older and had experience dancing and following other dancers ($E2_{Older\ Dancers}$), on each observation day we saw multiple $E1_{First\ Dances\ naive}$ bees following waggle dancers for natural food sources. In all control colonies, we had a marked cohort of bees of known age and likewise observed that they followed waggle dances before they performed their first dances ($C1_{First\ Dances}$;

Table 1. Summary of statistical results for all experiments. Colony type is either experimental (E) or control (C), and time point refers to (1) the first dances of bees or (2) subsequent dances of the same bees observed 20 days later.

Measure	Model R^2_{adj}	Colony type	Time point	Interaction, colony type by time point
Food direction				
Divergence angle	0.12	$F_{1,30} = 5.85$, $P = 0.02$	$F_{1,34} = 12.93$, $P = 0.001$	$F_{1,34} = 1.52$, $P = 0.23$
Food distance				
Waggle duration	0.79	$F_{1,32} = 157.20$, $P < 0.0001$	$F_{1,34} = 0.67$, $P = 0.42$	$F_{1,34} = 1.32$, $P = 0.26$
Waggle duration range error	0.34	$F_{1,30} = 20.08$, $P = 0.0001$	$F_{1,34} = 14.99$, $P = 0.0005$	$F_{1,34} = 0.09$, $P = 0.77$
Waggle duration CV	0.02	$F_{1,30} = 0.03$, $P = 0.86$	$F_{1,34} = 10.18$, $P = 0.003$	$F_{1,34} = 0.28$, $P = 0.60$
Number of waggles per waggle run	0.57	$F_{1,27} = 88.26$, $P < 0.0001$	$F_{1,34} = 1.46$, $P = 0.24$	$F_{1,34} = 1.01$, $P = 0.32$
Number of waggles per waggle run CV	<0.001	$F_{1,28} = 0.87$, $P = 0.36$	$F_{1,34} = 3.83$, $P = 0.06$	$F_{1,34} = 0.94$, $P = 0.34$
Return flight time	0.52	$F_{1,29} = 8.56$, $P = 0.007$	$F_{1,34} = 22.80$, $P < 0.0001$	$F_{1,34} = 12.48$, $P = 0.0012$
Food quality				
Number of waggle runs	0.56	$F_{1,30} = 4.99$, $P = 0.03$	$F_{1,34} = 21.58$, $P < 0.0001$	$F_{1,34} = 1.35$, $P = 0.25$
Return-phase duration	0.12	$F_{1,30} = 11.68$, $P = 0.002$	$F_{1,34} = 15.15$, $P = 0.0004$	$F_{1,34} = 2.54$, $P = 0.12$
Return-phase CV	0.03	$F_{1,31} = 0.13$, $P = 0.72$	$F_{1,34} = 0.60$, $P = 0.45$	$F_{1,34} = 0.05$, $P = 0.82$
Dance quality				
Disorder proportion	0.08	$F_{1,30} = 7.35$, $P = 0.011$	$F_{1,34} = 20.43$, $P < 0.0001$	$F_{1,34} = 6.46$, $P = 0.02$
Number of followers	0.76	$F_{1,31} = 180.07$, $P < 0.0001$	$F_{1,34} = 49.60$, $P < 0.0001$	$F_{1,34} = 17.46$, $P = 0.0002$

9.9 ± 1.0 days old) and continued to follow waggle dances over the next 20 days. All statistical results are reported in Table 1.

Food direction and distance

$E1_{First\ Dances\ naive}$ bees had significantly greater divergence angles (higher directional error) that decreased when they became $E2_{Older\ Dancers}$ bees [Tukey honestly significant difference (HSD) test, $P < 0.05$, Fig. 1B]. The dances of $C1_{First\ Dances}$ and $C2_{Older\ Dancers}$ bees did not have significantly different divergence errors.

The dances of $E1_{First\ Dances\ naive}$ and $E2_{Older\ Dancers}$ bees had longer waggle run durations than those of $C1_{First\ Dances}$ or $C2_{Older\ Dancers}$ bees (Tukey HSD test, $P < 0.05$, Fig. 2), suggesting that distance encoding was disrupted when bees could not follow experienced dancers and that disruption persisted even after they had more practice dancing and following other dancers. The reasons for this disruption are unclear, but $E1_{First\ Dances\ naive}$ foragers had longer return flight times than those of all other bee types (Tukey HSD test, $P < 0.05$). If $E1_{First\ Dances\ naive}$ bees thereby experienced

greater retinal optic flow, this should translate into longer waggle run durations (21). However, when the same bees were 20 days older, they had shorter flight durations and yet persisted in making the same distance-encoding errors.

The waggle duration range error was significantly higher in the dances of $E1_{First\ Dances\ naive}$ bees than in those of $C1_{First\ Dances}$ or $C2_{Older\ Dancers}$ bees (Tukey HSD test, $P < 0.05$), although it was not different between $E1_{First\ Dances\ naive}$ and $E2_{Older\ Dancers}$ bees, again suggesting a lifetime disruption of distance communication as a result of our treatment. In accordance with the waggle duration trends, the dances of $E1_{First\ Dances\ naive}$ and $E2_{Older\ Dancers}$ bees had more waggles per waggle run than those of $C1_{First\ Dances}$ or $C2_{Older\ Dancers}$ bees (Tukey HSD test, $P < 0.05$). There were no significant differences between coefficients of variation (CV) for waggle run duration or the number of waggles per waggle run (Tukey HSD test, $P > 0.05$).

Food quality

Bees signal higher-quality food relative to colony needs by increasing the number of waggle runs

per dance and performing shorter return phases (*11*). In general, our dancers tended to signal a higher value for identical sucrose solutions when their colonies were older and larger (E2$_{\text{Older Dancers}}$ and C2$_{\text{Older Dancers}}$ phases) than when their colonies were smaller and younger (Fig. 3A, E1$_{\text{First Dances naive}}$ and C1$_{\text{First Dances}}$ phases), perhaps reflecting greater colony need. The dances of E2$_{\text{Older Dancers}}$ bees had significantly more waggle runs than those of E1$_{\text{First Dances naive}}$ bees, but in control colonies there were no significant differences between the first waggle dances of bees and their waggle dances 20 days later (Tukey HSD tests, $P > 0.05$). Return-phase durations were only shorter for C2$_{\text{Older Dancers}}$ bees as compared with all other forager types (Tukey HSD tests, $P < 0.05$). There were no significant differences in return-run duration CV (Tukey HSD test, $P > 0.05$).

Dance quality

The dances of E1$_{\text{First Dances naive}}$ bees were significantly more disordered than the dances of E2$_{\text{Older Dancers}}$, C1$_{\text{First Dances}}$, or C2$_{\text{Older Dancers}}$ bees (Tukey HSD test, $P < 0.05$, Fig. 3B). The number of dance followers per dance was significantly lower for experimental colonies than for control colonies (Tukey HSD test, $P < 0.05$), but was not different between E1$_{\text{First Dances naive}}$ and E2$_{\text{Older Dancers}}$ bees. Increasing dance disorder was positively correlated with higher divergence angle errors for E1$_{\text{First Dances naive}}$ and C2$_{\text{Older Dancers}}$ bees ($F_{1,16} \geq 4.72$, $P \leq 0.045$) but not for E2$_{\text{First Dances}}$ or C1$_{\text{First Dances}}$ bees ($F_{1,16} \leq 0.43$, $P \geq 0.52$, Fig. 3C).

Our results suggest that social signal learning can improve waggle dancing. The dances of E1$_{\text{First Dances naive}}$ bees who could not follow dances before they first danced had greater divergence angle errors, signaled greater distances, and were significantly more disordered than those of C1$_{\text{First Dances}}$ bees that were exposed to waggle dancing. Once the same bees were older and had experience with dance following and dancing (E2$_{\text{Older Dancers}}$), they significantly decreased divergence angle errors and performed more orderly dances. However, they were never able to produce normal distance encoding. Greater age, more experience following dances, additional practice with flying and foraging, or a combination of these factors could account for the improvements between E2$_{\text{Older Dancers}}$ and E1$_{\text{First Dances naive}}$ dances. Control bees improved by reducing distance range errors only when they were 20 days older (C2$_{\text{Older Dancers}}$ versus C1$_{\text{First Dances}}$). Following experienced dancers before they first danced was sufficient for C1$_{\text{First Dances}}$ bees to correctly order their dances with the lower number of directional errors typical of older, experienced bees.

Why should honey bees use social learning to improve their waggle dancing? Learning is a useful way to refine behaviors for local con-
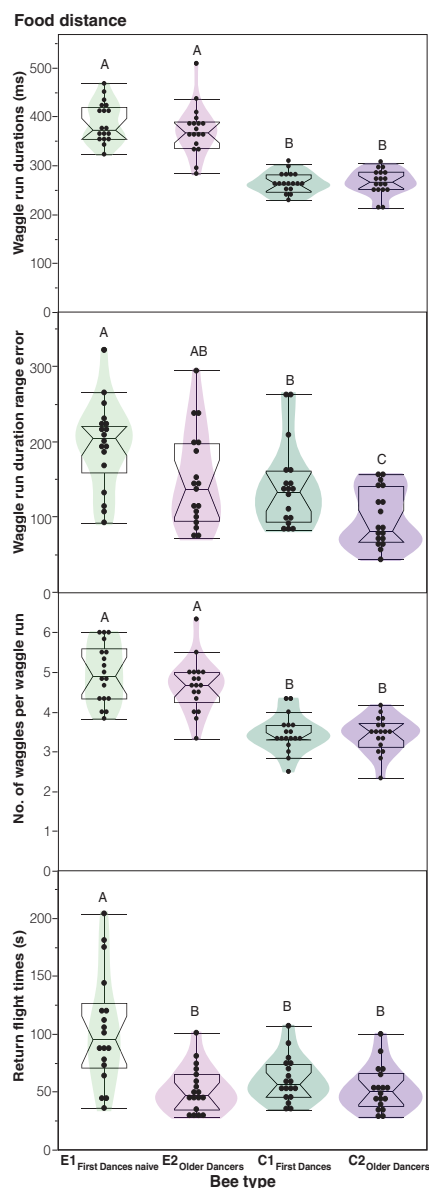
Fig. 2. Naive dancers that could not follow other dancers had disrupted distance encoding (waggle run durations and the number of waggles per waggle run) that persisted throughout their lifetimes. However, return flight times in experimental colonies significantly declined with experience. Different letters indicate significant differences.

ditions. We suggest that the distinct topologies of each colony's dance floor make it advantageous for novice dancers to learn from more experienced ones. Another possibility is that experienced dancers could transmit to nestmates distance encodings that are based on local optic flow. Theoretically, distance encodings should be optimized according to the environment: the locations of food and the amount of optic flow that foragers experience when flying to this food. Because honey
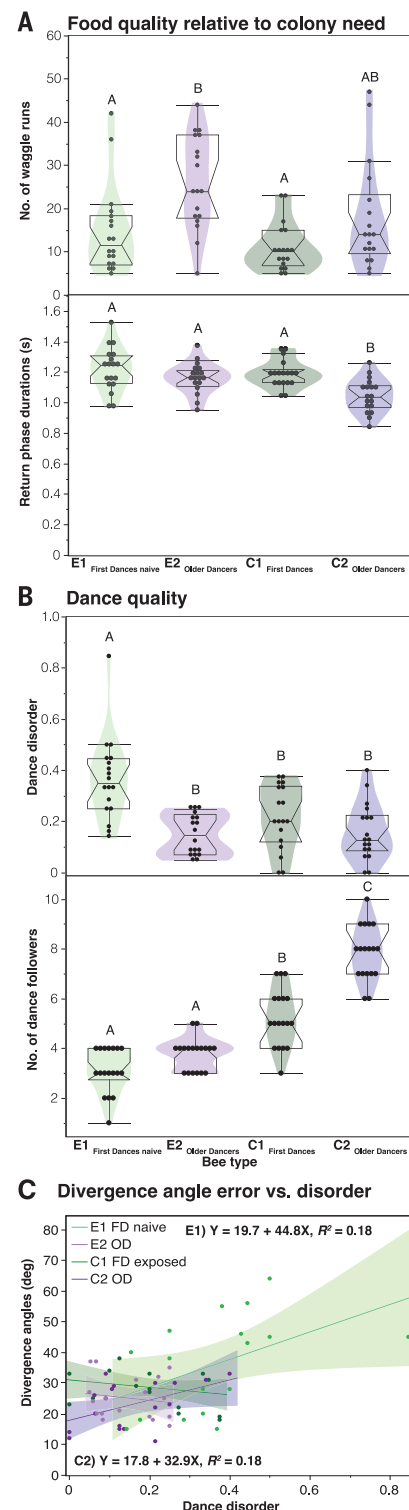
Fig. 3. Dance disorder was highest in naive first dancers and was positively correlated with angular error. Between groups, there were changes in (**A**) the communication of food quality and (**B**) dance quality and the number of dance followers (different letters indicate significant differences). (**C**) Directional error was positively correlated with dance disorder in E1$_{\text{First Dances naive}}$ and C2$_{\text{Older Dancers}}$ bees.

bee species can inhabit very different environments, distance encodings can be significantly different between species (*14*) and within species for *Apis florea* (*22*) and *Apis mellifera* (*23*). Given the imprecision inherent in waggle dances, the importance of these differences is not clear. Schürch *et al.* (*24*) compared the distance encodings of *A. mellifera* dancers in environments with different optic flow levels and found significant differences in the encoding line intercepts but not in the slopes. Our results indicate that we permanently altered distance encoding in our experimental colonies: After our treatment, novice dancers continued to make the same distance-encoding errors even near the end of their adult lives (*25*) despite decreasing their directional errors and dance disorder. Some aspects of the waggle dance can evidently be altered in young bees and are irreversible. Thus, we argue that the cultural modification and transmission of signals may be possible in social insects.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.ade1702
Materials and Methods
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Table S1
Movies S1 to S2
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MDAR Reproducibility Checklist

View/request a protocol for this paper from *Bio-protocol*